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A LINEAR PROGRAMMING MODEL OF DIET CHOICE OF FREE-LIVING BEAVERS

by

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ABSTRACT

Linear programming has been remarkably successful in predicting the diet choice of generalist herbivores. We used this technique to test the diet choice of free-living beavers (*Castor fiber*) in the Biesbosch (The Netherlands) under different foraging goals, *i.e.* maximization of intake of energy, nitrogen, phosphorus or sodium, or minimization of feeding time. Three food types were distinguished, *i.e.* woody food, herbs and roots of monocots. We assessed forage quality by measuring the dry matter, energy and mineral contents of the food plants as well as food intake rates, digestibility and metabolisability in captive beavers.

Actual diet was in accordance with the predicted food choice in the summer when the beavers were minimizing feeding time by mainly eating woody food. However, in the winter and spring, the beavers were predicted to feed upon non-woody food, whereas they (again) nearly exclusively ate woody food. The major reasons for this discrepancy might be: (1) the foraging constraints were inappropriate, (2) the foraging goals were inadequately defined, or (3) the beavers were not foraging optimally. We suggest that future work should take some additional constraints and foraging goals into account.

KEY WORDS: optimal foraging, nutrition, re-introduction, *Castor fiber*, The Netherlands.

INTRODUCTION

Because the tissue composition of plants and animals differ considerably, herbivores might need a balanced diet to meet their nutritional requirements (CRAWLEY, 1983). A number of studies have indicated that both American (*Castor canadensis* Kuhl) and Eurasian beavers (*C. fiber* Linneaus) eat a great deal of herbs in spring and aquatics in summer (NORTHCOTT, 1971; SVENDSEN, 1980; BELOVSKY, 1984b;

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ROBERTS & ARNER, 1984; HISTØL, 1989); SIMONSEN (1973) showed that aquatics can also make up a large proportion of their diet in winter. Hence, beavers typically have a mixed diet, and therefore are suitable animals to study the role of the nutritional quality of plants on diet choice in generalist herbivores.

Up to now, only deciduous woody food is considered essential to beavers (NOVAK, 1987). It is unclear whether non-woody food plants are a substitutable or compementary part of the beavers' diet. In the latter case, the beaver's fitness will be greater on mixed diets than on single species diets (RAPPORT, 1980). Indeed, ROBERTS & ARNER (1984) suggest that the high proportion of successful breeding pairs in the southeast of the United States is a result of their mixed diet. Herbs are generally protein-rich, and aquatics contain much sodium (*e.g.* DOUCET & FRYXELL, 1993). It may thus be hypothesized that beavers feed upon herbs and aquatics to meet their protein and sodium requirements, respectively.

In a linear programming problem, a goal is maximized (or minimized) subject to (linear) constraints. Therefore, unlike other models, linear programming models permit simultaneous treatment of energy and other nutrients in explaining diet choice. This is why these models have been so successful compared to other models of diet choice in herbivores, provided that food is classified in broad categories (BELOVSKY, 1984a; BELOVSKY & SCHMITZ, 1991).

Linear programming has previously been applied to American beavers. BELOVSKY (1984b) studied food choice of beavers on Isle Royale in summer, and showed that the observed mixed diet of woody food and aquatics more closely resembled the one predicted by maximization of the rate of energy intake than by minimization of feeding time. No sodium constraint was needed to correctly predict the proportions of aquatics in the diet. The beavers seemed to eat sufficient aquatics to make specific consumption for sodium redundant. DOUCET & FRYXELL (1993) successfully predicted the preference rank order of woody food plants in captive beavers. However, the only non-woody food in the test, the water lily *Nymphaea odorata*, was actually much more preferable than predicted. Although water lily contained an order of magnitude more sodium than the woody species, this could not explain the discrepancy as sodium intake appeared sufficient on a diet without water lily.

In order to provide a further field test of an optimal foraging model of beavers, we studied the diet choice of Eurasian beavers in the National Park the Biesbosch (51°45′N, 4°50′E) in the Netherlands. Here the animals were re-introduced after an absence of 200 years (BROEKHUIZEN *et al.*, 1992). The animals were trapped along the Elbe,

Germany (51°45′N, 12°45′E), and translocated to the Biesbosch. Six to 14 beavers were released yearly (NOLET & ROSSELL, 1994), and foraging behaviour of these animals was studied during their first year in the Biesbosch.

We first present measurements of the nutritional quality of the food plants available in the Biesbosch. We then give estimates of model parameters based on work with animals in captivity. Subsequently, the linear programming model is formulated using a variety of foraging goals and constraints. Finally, we present field tests with free-living animals.

METHODS

Chemical analysis of food plants

We sampled the most frequently eaten food plants of each food type, collecting samples of eight specimens per species in four seasons, namely in March (prior to the onset of the sapstream), April (just after the start of the growth season), June and September. In March and June, we sampled five tree species belonging to the Salicaceae family (*Populus x canadensis, Salix alba, S. dasyclados, S. triandra* and *S. viminalis*). In April and September, only the first three species mentioned were sampled. We took bark by stripping it from a branch 2 cm in diameter. From April onwards, we also cut twigs at a diameter of 0.5 cm, and collected the twigs with adhering leaves, and above-ground parts of the herbs *Anthriscus sylvestris, Urtica dioica, Heracleum sphondylium* (April and June) and *H. sphondylium* and *Bidens frondosa* (September). Roots of the monocots *Iris pseudacorus* and *Phragmites australis* were dug out in all seasons.

In August, we collected dead twigs at nine locations where we regularly observed beavers eating such twigs which they obtained by diving to the bottom of a creek.

Samples were weighed, frozen at -20°C shortly after collection, and subsequently dried to constant weight at 70°C. The proportion of dry matter (dm) was calculated as dry weight divided by fresh weight. Ash was measured gravimetrically after exposure to 375 or 550°C. N was measured according to the standard Kjeldahl method. After destruction of samples with HNO_3 in a microwave or, according to Fleischman, with a 1:1 mixture of HNO_3 and H_2SO_4, Mg and Ca were measured by atomic adsorption spectrometry (AAS), K by atomic emission spectrometry (AES), and Na by AAS or AES. P was measured colorimetrically on an auto analyser. The analytical results from our laboratory were amply within the 90%-confidence intervals around the averages of all laboratories participating in the International Plant-analytical Exchange (V.J.G. Houba, Wageningen Agricultural University, Wageningen). Energy content (E) was measured by bomb-calorimetry. E and mineral concentrations were ln-transformed, and ash and dm were logit-transformed to approximate normal distributions. Outliers were identified and omitted from further analysis as explained in an earlier paper (NOLET *et al.*, 1994). Differences in nutrient concentrations among food types and seasons were tested with a two-way ANOVA.

Parameter estimation with captive beavers

Four beavers were maintained in captivity for up to one year. The beavers were 1.5 to 5 years old, and weighed 12 to 21 kg. Beavers were housed singly in a 14 m^2 pen with a concrete floor and a 3.8 × 0.4 × 0.4 m deep water channel. Each beaver slept in a

wooden box, which we had put on top of a scale (Mettler TE 60/J) in order to monitor body mass. The scale was calibrated each morning with a 10 kg weight.

On five days, we video-taped the beaver while inside the wooden box with a timelapse recorder. From these tapes we determined the time spent on coprophagy, *i.e.* eating of faeces from the cloaca (Tc, h/day), as the duration between the first and the last faeces ingested.

A feeding trial consisted of 3-4 days on which a single feed was offered in the evenings. For food which dried out (twigs with young leaves and herbs) a subsample was put out of reach of the beaver in the same room. We calculated fresh intake (Iwet, g/day) as the difference between offered food and food remains, corrected for desiccation when appropriate.

The beaver was observed with a night-scope, and the time it spent gnawing (Tg, h/day) during one whole night per feeding trial was measured. Fresh food intake rate (Iwet, g/h) was calculated as Iwet/Tg. In the spring and summer, woody food consisted of both bark and twigs with adhering leaves. In order to calculate the intake of bark and leaves separately, we used a Iwet of bark of 285 g/h (as measured by weighing non-leaved branches before and after a feeding night where bark was stripped instead of gnawed from the wood).

The beavers always defaecated in the channel, which we drained in the morning. Preliminary measurements of the food passage rate through the gastro-intestinal tract, using bark of *Salix alba* coloured with a basic fuchsin solution (Foose, 1982), gave a mean retention time of 12.4 h ± 2.6 S.E. (n = 3). We therefore started collection of the faeces from the second morning onwards (*i.e.* first collection 36 h after the start of the feeding trial) by seiving the faeces out of the water. Intact faeces floated on the water and were collected separately. A food sample and all the faeces were stored at -20°C, until they were dried to constant weight at 70°C. Gross energy content (E) of the food and of the intact faeces was measured with a Gallenkamp bomb-calorimeter. We calculated apparent digestibility of dry matter (DDM) as:

$$\text{Apparent DDM} = (\text{Iwet} \times \text{dm} - \text{Fdry}) / (\text{Iwet} \times \text{dm}),$$

where Fdry is the weight (g) of the dry faeces. Apparent DDM was measured for 2-3 consecutive days and averaged to overcome day-to-day variation in food consumption and faeces production. In order to calculate the apparent digestibility of bark and leaves separately, we assumed a DDM of bark of 0.55 (the DDM of bark in winter).

Metabolisable energy intake (MEI) is the gross energy intake (GEI, kJ/day) minus the energy lost in the faeces, urine and gas. The energy content of the faeces (Ef) was measured (Ef = E [kJ g_{dry}] × Fdry [g_{dry}/day]). The energy content of the urine (Eu) was approximated from the nitrogen concentration (N, g/kg_{dry}) of the food (Blaxter, 1989):

$$\text{Eu (kJ/day)} = \text{GEI} \times (0.156 \times \text{N} + 1.6) / 100.$$

We did not measure N in the food samples of the feeding trials, but took the N value of the same kind of food from the food analysis. The N concentration of carrots was taken from literature (16.0 g/kg_{dry}; Jansen, 1977). We neglected gas production because beavers are hindgut-fermenters in which gas production is negligible in contrast to ruminants. The metabolisability or assimilation quotient (q) is the proportion of GEI actually absorbed by the animal (Blaxter, 1989), which can now be calculated as:

$$q = (\text{GEI} - \text{Ef} - \text{Eu}) / \text{GEI}.$$

Differences between woody food in winter and summer, and between woody and non-woody food were tested with a separate-variance t-test.

Model formulation

The three food types considered (*i.e.* woody food, herbs and roots of monocots) were spatially separated, growing on different banks (NOLET & ROSELL, 1994). A distribution map of the banks is provided by NOLET (1993). In general, the food types were therefore not simultaneously encountered, and we could ignore differences in encounter rates (BELOVSKY & SCHMITZ, 1991). We used linear programming (Scicon MicroLP Optimiser) to model the optimal diet choice in winter, spring and summer under different foraging goals: maximization of metabolisable energy intake (MEI), nitrogen, phosphorus or sodium intake and minimization of feeding time.

We formulated the following limits (constraints which cannot be exceeded) and requirements (constraints which should be surpassed):

(1) Assimilation limit. MEI is constrained by the digestive tract's capacity to assimilate energy (WEINER, 1992). WEINER (1989) gathered data on MEI from several mammal species at peak lactation, and related this to body mass (M):

$$\text{MEI (kJ/day)} = 1815\ M^{0.664}.$$

M of the released adult beavers (>3 year old) averaged 23.0 kg ± 0.6 S.E. (n = 17). We used this body mass in our model. Substitution gives the assimilation limit (A):

$$14557\ \text{kJ/day} \geq \Sigma\ \text{Idry}_i \times q_i \times E_i,$$

where the subscripts i denote a specific food type in a specific season.

(2) Foraging time limit. Beavers produce hard and soft faeces, of which the soft ones are re-ingested. The production of the two types of faeces is temporally separated, and the faecal re-ingestion ('coprophagy') only takes place while inside the den (BUECH, 1984). We assumed that beavers spent a fixed time per day on coprophagy. By estimating the length of the inactive period from the duration of coprophagy instead of the observed time span which free-living beavers spent in their dens, we obtained an independent estimate of the foraging time limit.

NOLET & ROSELL (1994) observed that the body temperature of beavers dropped while swimming and rose again while grooming on the bank. Based on this observation we inferred that beavers underwent a requisite body temperature cooling-heating cycle during swimming. The heating period on the bank was determined by cooling ($\dot{C}$) and heating rates ($\dot{H}$), both depending on water temperature (MACARTHUR & DYCK, 1990). The potential daily foraging time (Tf_{max}) was estimated from the observed time spent on coprophagy (6.6 h/day) and the time in water (Tw) (excluding the first two years of the study in which the beavers spent much time exploring their new surroundings; NOLET & ROSELL, 1994) as:

$$Tf_{max}\ (\text{h/day}) = 24 - 6.6 - (1 + \dot{C} / \dot{H}) \times Tw.$$

The foraging time limit becomes:

$$Tf_{max}\ (\text{h/day}) \geq \Sigma\ \text{Idry}_i / (\dot{I}\text{wet}_i \times dm_i \times g).$$

(3) Metabolisable energy requirement. During maintenance, the metabolisable energy requirement is equal to the daily energy expenditure (DEE, kJ/day). In order to estimate DEE, we multiplied the time spent on each behaviour by the metabolic rate corresponding to the specified behaviour and ambient temperature. However, no metabolic data are available for Eurasian beavers. Following the procedure described in detail in NOLET & ROSELL (1994), we therefore used measurements of metabolic rates in captive American beavers (COLES, 1967; MACARTHUR, 1989; MACARTHUR & DYCK, 1990), and an allometric model of swimming costs (VIDELER & NOLET, 1990). The

swimming costs were corrected for the energy lost in a wake when swimming at the surface and temperature effects using measurements in the muskrat (*Ondatra zibethicus*) (FISH, 1982, 1983). As ambient temperatures, we used air temperatures from the weather station Gilze-Rijen at approximately 20 km from the Biesbosch, and the water temperatures which were measured weekly by the Water Storage Corporation in the Biesbosch.

Our calculated DEE is a minimum estimate of the real DEE because all costs are based either on resting conditions without arousal or on swimming at optimum speed which, per definition, is the speed at which the animal spends the minimum energy per distance moved. Thus, during maintenance, the metabolisable energy requirement (ME) can be formulated as:

$$DEE\ (kJ/day) \leq \Sigma\ Idry_i \times q_i \times E_i.$$

In ungulates, the additional energetic costs of the last phase of pregnancy are about 40% of their basal metabolic rate (BMR) (ROBBINS, 1983). BMR was measured by MACARTHUR (1989) in *Castor canadensis*, and equalled $4.18 \times M^{0.67}$ W, so that in adult beavers (23 kg) 40% of BMR is 1180 kJ/day. The ME during gestation is thus:

$$DEE + 1180\ (kJ/day) \leq \Sigma\ Idry_i \times q_i \times E_i.$$

The ME during lactation is identical to the assimilation limit (A) apart from the relational operator ($\leq$ instead of $\geq$):

$$14557\ (kJ/day) \leq \Sigma\ Idry_i \times q_i \times E_i.$$

(4) Phosphorus and (5) sodium requirements. The nutrient requirements of beavers have not been measured. We therefore gathered published data on the required minimum daily intake of P and Na in other herbivorous mammals, which were either assessed empirically (by measuring the minimum nutrient concentration in the food at which no symptoms of deficiencies occur) or factorially (by analysing the nutrient budget). In the latter case, an estimate of the efficiency with which the animal absorbs the nutrient from the food is needed: for P, we used the estimates reported by the authors, and for Na, we assumed an efficiency of 100%. For maintenance, gestation and lactation, respectively, we derived the following allometric relationships between the daily P requirement (R_p) and body mass (M, kg) (fig. 1a):

$$R_p\ (g/day) = 0.0228 \times M^{1.01}\ (r^2 = 0.99,\ n = 5),$$
$$R_p\ (g/day) = 0.172 \times M^{0.773}\ (r^2 = 0.98,\ n = 8),$$
$$R_p\ (g/day) = 0.259 \times M^{0.814}\ (r^2 = 0.98,\ n = 7).$$

For a hypothetical 23-kg beaver, the daily requirement increases from 0.55 g P/day during maintenance to 1.94 and 3.33 g/day during gestation and lactation, respectively.

During maintenance, gestation and lactation, respectively, the sodium requirement (R_{Na}) increased with body mass as (fig. 1b):

$$R_{Na}\ (g/day) = 0.00523 \times M^{0.939}\ (r^2 = 0.91,\ n = 10),$$
$$R_{Na}\ (g/day) = 0.0169 \times M^{0.744}\ (r^2 = 0.92,\ n = 7),$$
$$R_{Na}\ (g/day) = 0.0536 \times M^{0.790}\ (r^2 = 0.90,\ n = 7),$$

An adult beaver thus requires 0.099, 0.174 and 0.638 g Na/day, during maintenance, gestation and lactation, respectively.

Thus, the phosphorus and sodium requirements are, respectively:

$$R_p\ (g/day) \leq \Sigma\ Idry_i \times P_i/1000,$$
$$R_{Na}\ (g/day) \leq \Sigma\ Idry_i \times Na_i/1000,$$

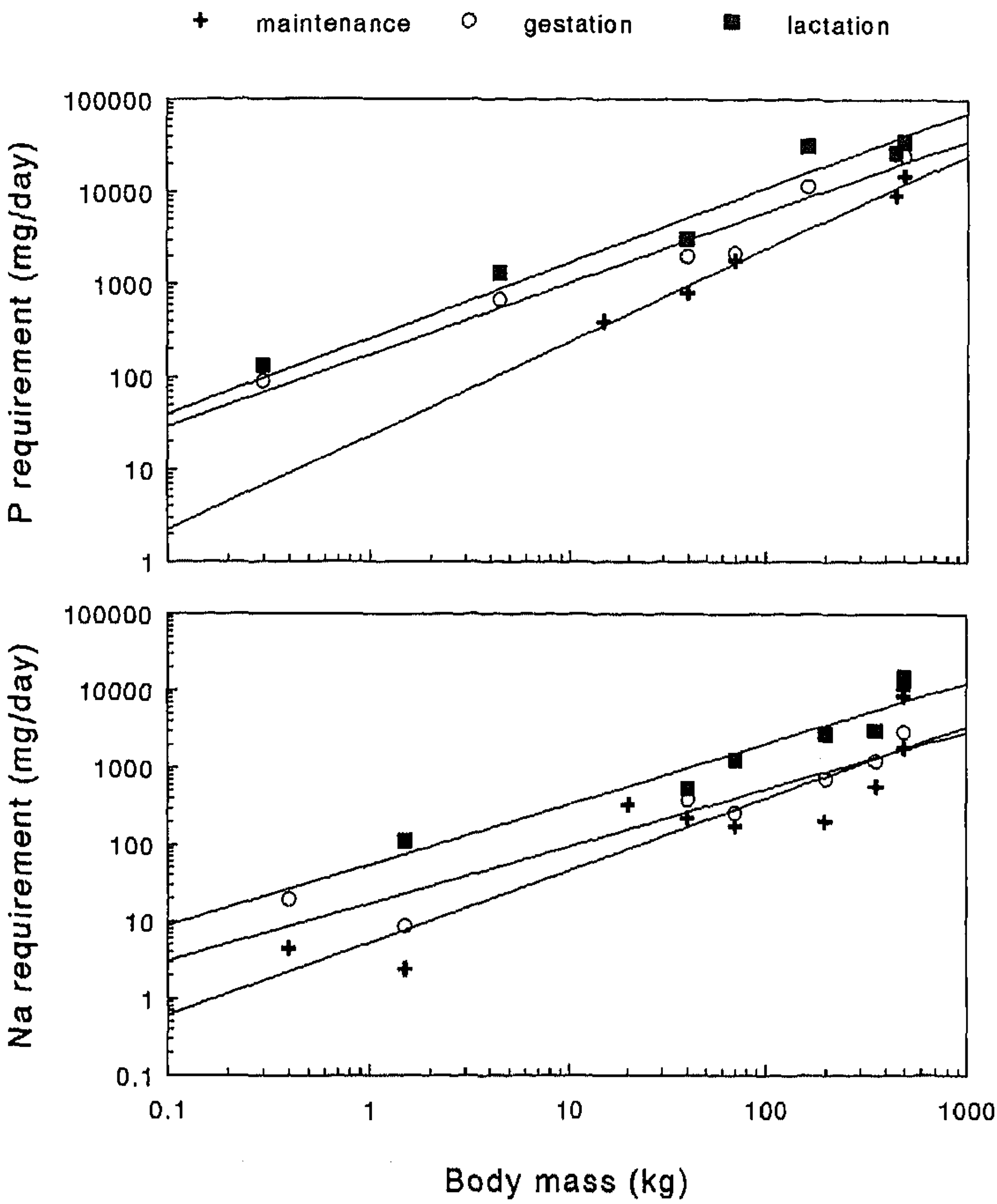


Fig. 1. (Upper panel) Phosphorus requirement (g/day) in a number of herbivorous mammals during maintenance, gestation and lactation: mouse, rat (NRC, 1978b), rabbit (NRC, 1977), dwarf goat (AKINSOYINU, 1986), white-tailed deer (*Odocoileus virginianus*) (WEEKS & KIRKPATRICK, 1976; PLETSCHER, 1987), pig (NRC, 1988), horse (NRC, 1978a) sheep and cattle (ARC, 1980). (Lower panel) Sodium requirement (g/day) in herbivorous mammals during three conditions: meadow vole (*Microtus pennsylvanicus*) (HASTINGS *et al.*, 1991), guinea pig (APGAR *et al.*, 1992), showshoe hare (*Lepus americanus*) (BELOVSKY, 1984c), dwarf goat (MC SWEENEY & CROSS, 1992), white-tailed deer (WEEKS & KIRKPATRICK, 1976; PLETSCHER, 1987), moose (*Alces alces*) (BELOVSKY & JORDAN, 1981), sheep, pig, cattle and horse (AITKEN, 1976).

where P_i and Na_i are the phosphorus and sodium concentrations (g/kg_{dry}) of food type i.

A specific nitrogen (or protein) requirement was not used as an additional constraint, because the intake of N was adequate for all possible diets before the P requirement was met (based on a maintenance requirement of 0.28 g $N/kg_M^{0.75}$/day; NRC, 1978b; CORK, 1986).

Field observations

We observed the feeding behaviour of 31 beavers with implanted radio-transmitters (NOLET & ROSELL, 1994). The beavers were sequentially released in the Biesbosch in the autumn of 1988, 1989, 1990 and 1991. The life span of the transmitters was on average 1.2 years, and observations were carried out from November until September of each following year. The beavers were at least one year old, and the body mass M averaged 19.3 kg ± 0.9 S.E. (n = 31). None of these beavers were reproducing.

Beavers were tracked in the evening and at night, and observed with binoculars or, after darkness, infrared-binoculars or binoculars and a lamp. Time budgets were derived from the recorded behaviour at 15 minute intervals (NOLET & ROSELL, 1994). The daily time spent feeding (Tf, h/day) calculated in this way included selecting, gathering and gnawing the food. We used evening observations on a single female which could be observed at close range to correct Tf to obtain the daily time spent gnawing (Tg). On a dictaphone, we recorded both its behaviour at 15 minute intervals and its actual time spent gnawing the food by continuous observation. From the relationship between the proportion of the point observations spent feeding and the proportion of the time spent gnawing the food, we derived g = Tg/Tf, the proportion of the feeding time spent gnawing. We did not have detailed observations of the amount of time it took beavers to dig out roots, but from incidental observations we had the impression that digging out roots took as long as actually eating them.

We defined three food types: woody (bark and twigs with adhering leaves), above-ground parts of herbs, and roots of monocots. The time spent gnawing a specific food type was recorded in the evening until the focal animal was lost from sight for more than half an hour. This near-continuity of observation was required in order to avoid a pick-up bias, because the noisy feeding on woody food was more easily detected than the feeding on herbs or roots. Observations within a given season were summed to obtain proportions of time spent gnawing a given food type (f_i). The daily intake of dry matter (Idry) of a specific food type i per season was estimated as:

$$Idry_i\ (g_{dry}/day) = f_i \times g \times Tf \times dm_i \times Iwet_i,$$

where dm is the proportion of dry matter of the feed, and Iwet is the fresh food intake rate (g/h).

RESULTS

Chemical properties of food plants

The food types clearly had different nutrient concentrations. Mean dm, ash and mineral concentrations were all significantly different among food types and seasons (fig. 2 and table I). Only E did not show a seasonal trend (ANOVA, $p > 0.1$). Woody food was much less bulky than roots and herbs (fig. 2a), and contained more E than roots, with intermediate levels in herbs (fig. 2b). Herbs, on the other hand, were particularly rich in P (fig. 2c), and to a lesser extent in N (table I). Herbs also contained great concentrations of K, especially in spring (table I). Roots appeared to contain an order of magnitude more Na than woody species or herbs (fig. 2d). There was a significant interaction between food type and season in all food quality parameters,

TABLE I

Chemical analyses of food plants of beavers in the Biesbosch in four seasons: ash content (back-transformed mean values [y = exp(x)/(1 + exp (x))] in % of dry weight) and geometric mean mineral concentrations (g/kg_{dry}) (95%-confidence interval within parentheses; sample size is indicated within brackets when different from value in column).

season	*sample size*	*ash*	*K*	*Mg*	*Ca*	*N*
winter						
bark	40	7.2 (6.6-7.9) [39]	6.6 (5.9-7.5)	1.2 (1.1-1.3) [36]	18.7 (16.6-21.0)	12.7 (11.9-13.5)
roots	16	8.9 (7.5-10.5)	14.1 (12.4-16.1) [15]	1.2 (0.8-1.7)	3.7 (2.1-6.7)	13.8 (11.5-16.6)
spring						
bark	22	8.0 (7.4-8.7)	5.4 (4.7-6.2)	1.2 (1.0-1.4)	25.3 (23.1-27.6)	12.2 (10.9-13.7)
leaves	23	6.7 (6.1-7.3)	10.4 (9.1-11.7)	1.5 (1.4-1.7)	14.0 (12.3-16.1)	23.4 (21.1-25.8)
herbs	24	18.3 (16.2-20.5)	47.5 (35.5-63.5) [23]	2.9 (2.7-3.2) [20]	20.4 (17.5-23.7) [22]	45.0 (42.8-47.3)
roots	16	7.1 (6.3-8.1) [15]	11.8 (10.0-14.0)	1.2 (0.9-1.6)	3.9 (2.3-6.5)	12.0 (10.7-13.5) [15]
summer						
bark	22	7.5 (6.7-8.3)	3.7 (3.3-4.2)	1.2 (1.0-1.4) [21]	19.7 (17.0-22.8)	9.7 (9.0-10.4)
leaves	37	5.7 (5.2-6.3)	9.0 (8.1-9.9)	1.7 (1.5-1.8) [35]	9.8 (8.6-11.2)	19.9 (18.6-21.3)
herbs	23	11.7 (10.8-12.7)	28.2 (24.3-32.8)	2.6 (2.1-3.1)	17.8 (16.2-19.6)	16.6 (14.2-19.5)
roots	15	6.6 (4.1-10.3)	7.8 (6.0-10.0)	1.5 (1.1-1.9) [14]	5.2 (3.6-7.5)	8.4 (6.6-10.7)
autumn						
bark	24	7.6 (7.0-8.2) [22]	7.1 (6.5-7.8) [23]	1.2 (1.1-1.4)	21.1 (18.5-24.1) [23]	9.3 (8.5-10.2)
leaves	24	7.4 (6.8-7.9) [23]	9.0 (8.2-9.9)	2.3 (2.0-2.6)	16.9 (15.3-18.6)	15.1 (13.6-16.9)
herbs	16	10.4 (8.6-12.5)	29.6 (25.0-35.1)	2.9 (2.4-3.5)	12.6 (9.6-16.5) [14]	21.1 (18.5-23.9)
roots	16	9.2 (6.9-12.2)	12.0 (10.0-14.4)	1.4 (1.2-1.7)	4.9 (3.6-6.5)	8.0 (6.6-9.6)

indicating that food quality changed differently with season in the different food types. Both the rise in dm and drop in P and N concentrations during the year were more pronounced in leaves of woody species than in herbs, caused by the emergence of new herb species in the summer.

Dead twigs which beavers surfaced from the bottom of the creeks appeared to have significantly greater Na concentrations (g/kg_{dry}) (geometric mean 0.45, 95%-confidence interval 0.40-0.50, n = 9) than living bark (0.14, 0.11-0.17, n = 22) or leaves (0.26, 0.20-0.33, n = 22)

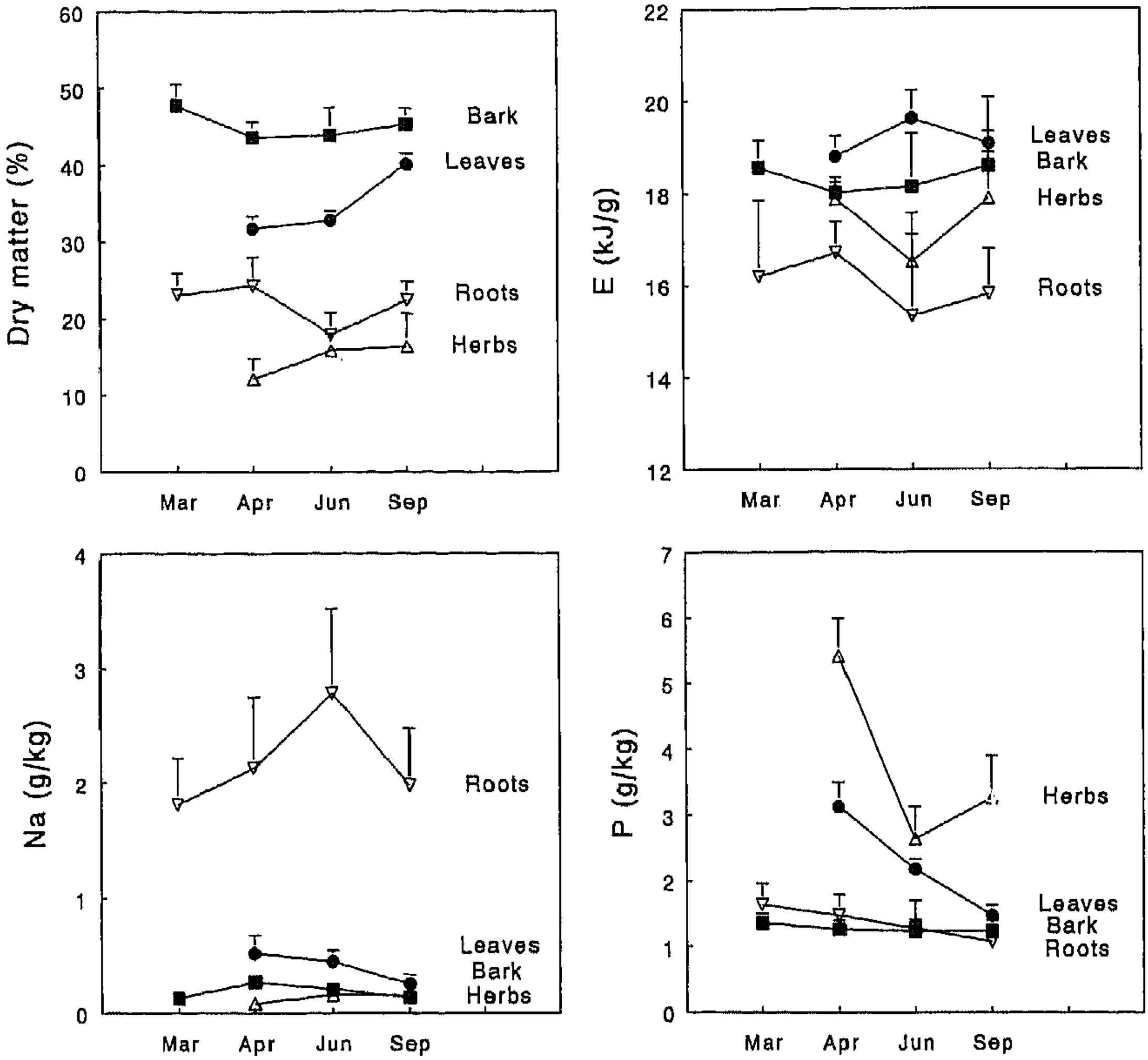


Fig. 2. (a) Back-transformed values of mean dry matter, and geometric means of (b) gross energy, (c) sodium and (d) phosphorus concentration of different food types during the year. Errors bars indicate upper 95%-confidence limit of mean. Sample size is given in table II.

in autumn. Potassium concentrations (g/kg_{dry}) were, on the contrary, much less in dead twigs (0.8, 0.7-1.0, n = 9) than in living bark (7.2, 6.5-7.8, n = 23) or leaves (9.0, 8.2-9.9, n = 24).

Feeding trials in captive beavers

The feeding trials were hampered by the beavers' reluctance to eat herbs and roots from the Biesbosch. The daily dry food intake (Idry) of herbs was only 0.9 $g/kg_M/day \pm 0.4$ S.E. (n = 17), and that of roots 1.0 $\pm$ 0.6 S.E. (n = 5). In order to obtain some figures about food intake rate and digestibility of herbs and roots, we offered a mixture of herb

TABLE II

Feeding parameters in captive beavers (mean ± S.D. or back-transformed mean values [y = exp(x)/(1 + exp(x))] with range within parentheses; sample size is given within brackets when different from preceding cell in the same row).

season	*dry intake Idry* ($g/kg_M/day$)	*fresh intake rate İwet* (g/h)	*apparent digestibility of dry matter DDM*	*metabolisability q*
winter				
bark	24.8 ± 4.9 [11]	213 ± 46 [5]	0.55 (0.41-0.66) [6]	0.52 (0.41-0.64)
spring/summer				
bark		285[a]	0.55[a]	0.48 (0.45-0.50) [5]
leaves		490 ± 121 [7]	0.78 (0.64-0.84)	0.72 (0.56-0.77)
woody	35.6 ± 7.9 [27]	416 ± 86 [7]	0.71 (0.61-0.75) [5]	0.65 (0.53-0.70)
herbs	13.5 ± 1.7 [4]	790 ± 138 [2]	0.77 (0.75-0.80) [3]	0.70 (0.65-0.75) [2]
roots	14.4 ± 3.8 [4]	1031 [1]	0.96 (0.91-0.98) [3]	0.92 (0.87-0.94)

[a] Assumed.

species from outside our study area, and used carrots instead of roots from monocots. The daily intake of these was an order of magnitude greater than of those from the Biesbosch (table II). Because of the small sample size, data on non-woody foods were lumped for statistical comparison with woody species.

In the summer, Idry of woody food was significantly greater ($p < 0.001$) than that of non-woody food (table II). The fresh food intake rate (İwet) of woody food, on the other hand, was less ($p < 0.05$) than that of non-woody food. Moreover, the digestibility (DDM) and assimilation (q) of woody food were also significantly less ($p < 0.05$) than those of non-woody food.

Winter bark was clearly a poor quality feed in terms of metabolisable energy intake rate: Idry, İwet, DDM and q were all significantly less ($p < 0.05$) than those of woody food in the summer (table II). In the winter, bark had to be gnawed from the wood, whereas in the spring and summer bark was easily stripped from the wood. İwet of bark in the winter was thus also significantly less ($p < 0.05$) than 285, the İwet of stripped bark.

Daily fresh food intake (Iwet) expressed in (kg_{wet}/kg_M) was negatively correlated with the proportion of dry matter (dm) of the food (r^2

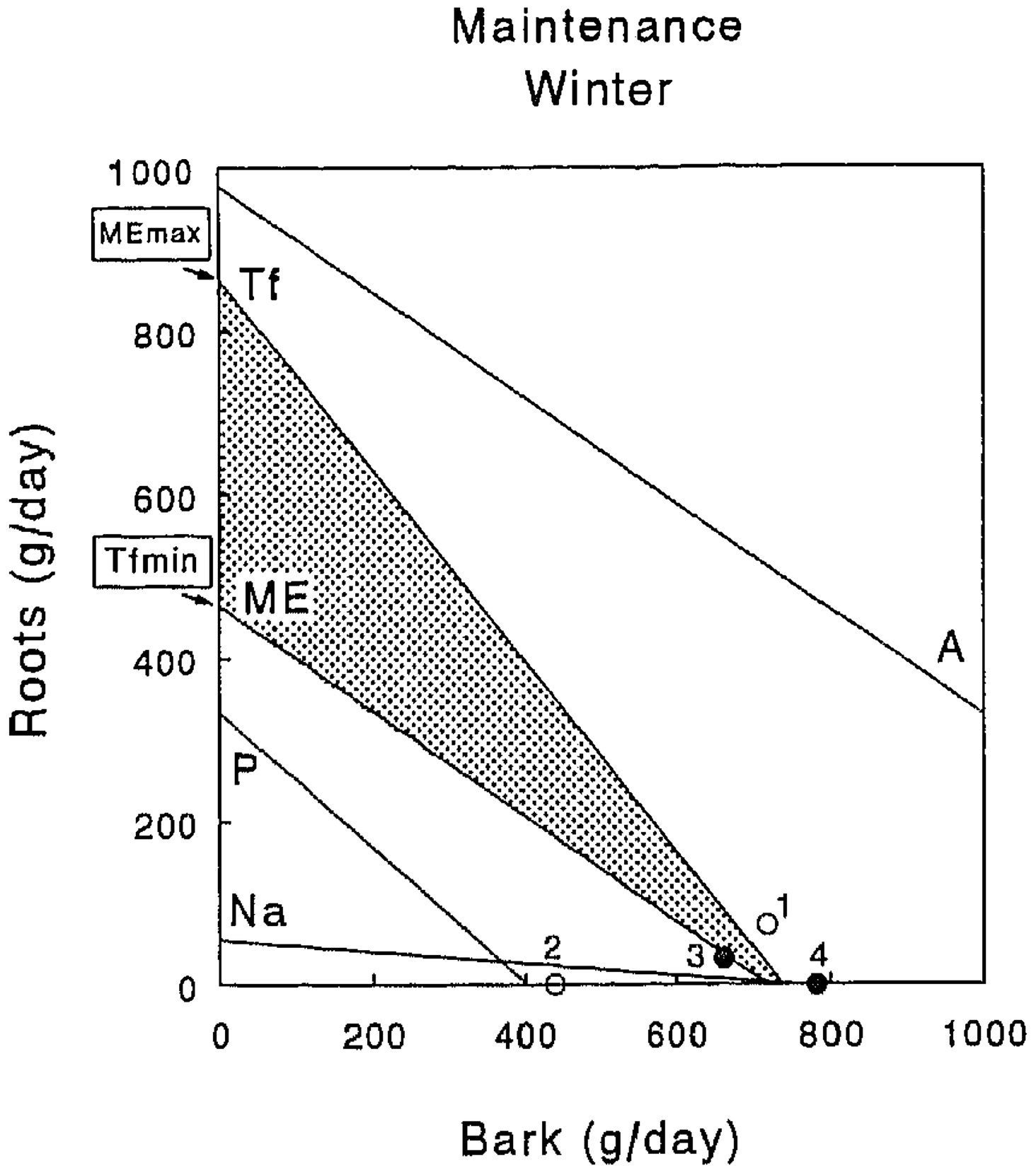
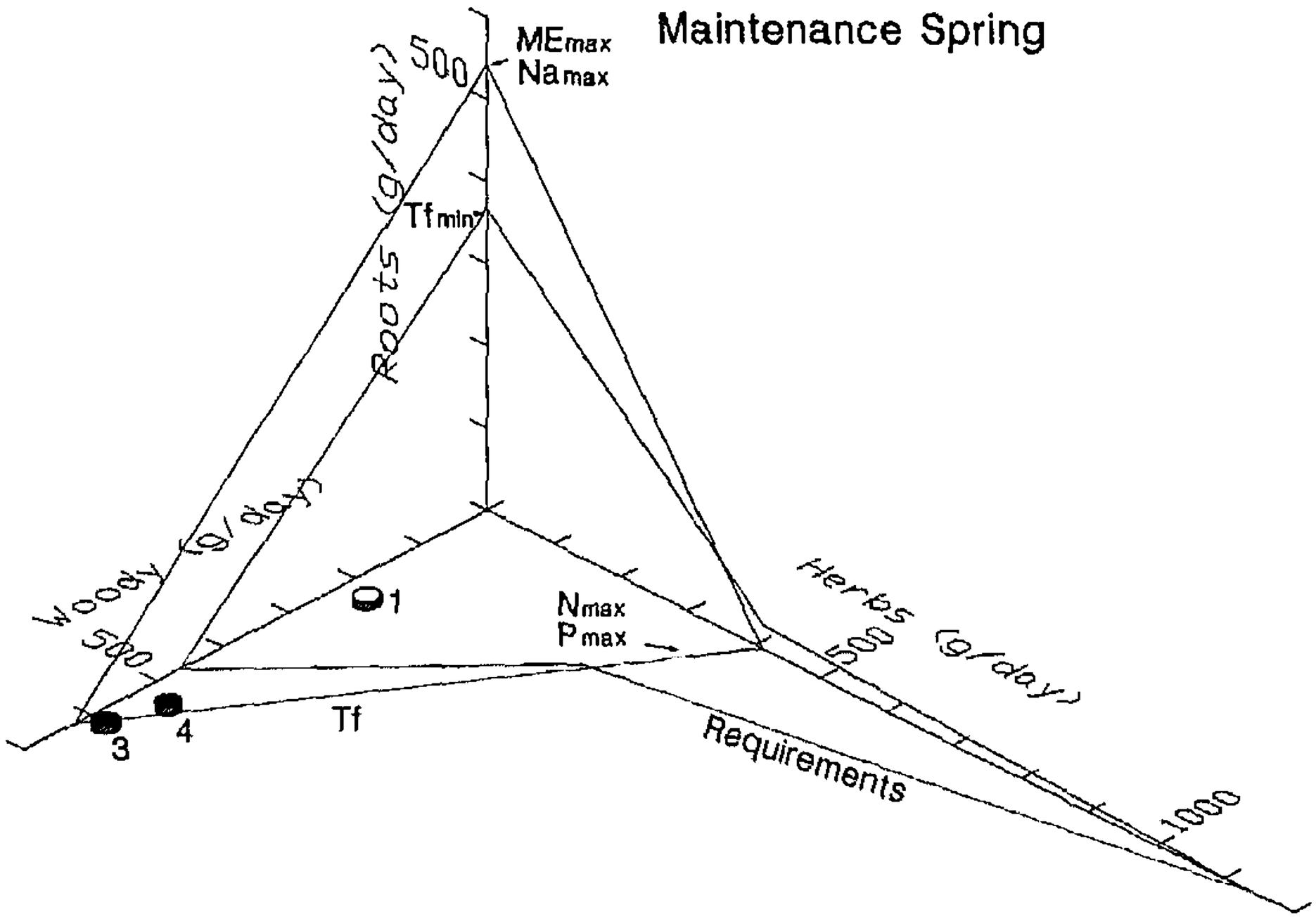


Fig. 3. Diet of adult beavers in the Biesbosch in winter, when beavers can choose between bark and roots of monocots. In order to satisfy the daily metabolisable energy, phosphorus and sodium requirements, the diet choice should be above the ME, P and Na lines, respectively. At the same time, the diet should not exceed the foraging time limit (Tf) or assimilation limit (A). The shaded area depicts the combinations which satisfy these conditions. Arrows indicate the diets predicted under different foraging goals; the optimum solutions under ME, N, P or Na maximization are identical. ○ and ● are the observed diets in the first and last two years of the study, respectively. In the second winter the beavers were exploring their new habitat.

= 0.39, $p < 0.001$, $n = 53$). It was positively correlated with apparent DDM ($r^2 = 0.54$, $p < 0.001$, $n = 53$). There was a large colinearity between apparent DDM and dm ($r^2 = 0.60$, $p < 0.001$, $n = 53$), which precluded the use of a multiple linear regression model with both apparent DDM and dm as dependent variables.

In the captive beavers, coprophagy was observed for a period of on average 6.6 h/day ± 1.1 S.D. ($n = 5$) whilst inside the artificial den. At more or less regular intervals of on average 72 min ± 45 S.D. ($n = 24$), the animal in the wooden box sat on its tail for 8 min ± 6 S.D. ($n = 29$), and ate feaces directly from the cloaca. This behaviour was never observed at night when the beavers were outside the wooden box.



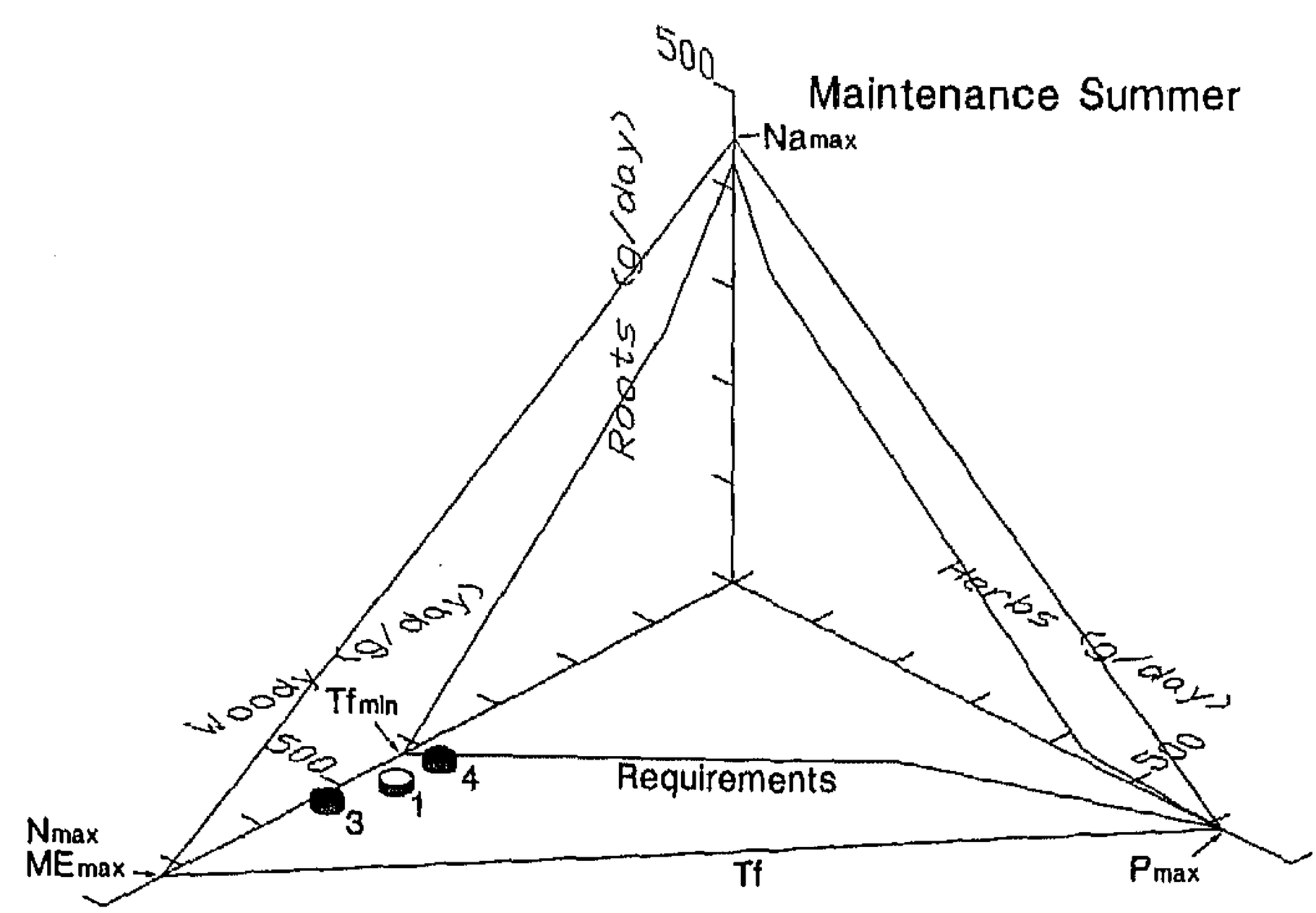


Fig. 4. Diet of beavers during maintenance conditions in (a) the spring and (b) the summer, when beavers can choose among woody food, herbs and roots. The 'requirements' plane is a composite of the ME, P and Na constraints, and the diet choice should be above this plane in order to satisfy the ME, P and Na requirements. At the same time, the diet should not be above the foraging time (Tf) or assimilation (A) planes. Arrows indicate the diets predicted under different foraging goals. The white draughtsmen indicates the observed diets in the first year of the study, when the beavers were exploring their new habitat; the black draughtsmen are the observed diets in the last two years of the study (no observations in the second year).

TABLE III

Feeding behaviour of free-living beavers in the Biesbosch in three seasons (mean ± S.E.).

season	*sample size*	*observed (h)*	*time active Ta (h/day)*	*foraging time Tf (h/day)*	*time spent gnawing food Tg (h/day)*	*proportion of foraging time spent gnawing food g*
winter	4	66.1	12.0 ± 0.4	7.7 ± 0.6	6.6 ± 0.8	0.85 ± 0.04
spring	3	36.9	10.0 ± 0.2	5.1 ± 0.5	3.5 ± 0.7	0.66 ± 0.07
summer	3	26.7	10.1 ± 0.4	5.0 ± 0.3	3.3 ± 0.3	0.68 ± 0.02

	proportion of time spent on gnawing food type i f_i x 100%			
	bark	*leaves*	*herbs*	*roots*
winter	97 ± 2			3 ± 2
spring	22 ± 0.5	64 ± 6	13 ± 5	1 ± 1
summer	45 ± 12	48 ± 12	6 ± 2	0.3 ± 0.2

Diet predicted by the linear programming model

In the winter, the beavers could choose between bark and roots. Bark had a greater gross energy (E) content than roots, but this was offset by its relatively poor assimilation (q). The proportion of dry matter consisting of neutral-detergent fibre was more than twice as large in bark of Salicaceae than in roots of *Iris pseudacorus* (S.E. van Wieren & B.A. Nolet, unpublished data). Beavers do not possess a special ability to digest these cell wall constituents (CURRIER *et al.*, 1960), and a large proportion of E of bark seemed locked in the cell walls. According to the linear programming model, the beavers should eat roots instead of bark if the beavers were striving to maximize intake of metabolisable energy, nitrogen, phosphorus and sodium, or if they were trying to minimize the foraging time (fig. 3).

In the spring, the beavers could choose among woody food, herbs and roots. Because one of the assumptions of the linear programming model applied here is that the beavers are not simultaneously searching for different food types (BELOVSKY & SCHMITZ, 1991), we did not distinguish between bark and twigs with adhering leaves. Instead we supposed that the beavers always ate these parts of woody species in the same proportion as observed, and calculated the nutritional quality of woody food accordingly. A diet of only roots was predicted under metabolisable energy or sodium maximization (fig. 4a). In order to

maximize the intake of nitrogen or phosphorus, the beavers should eat a mixed diet with mainly herbs.

In the summer, the quality (dm, E) of the roots of monocots decreased after the sprouting of their leaves. Consequently, the beavers were predicted to switch to woody food in order to maximize the metabolisable energy and N intake or to minimize the feeding time (fig. 4b). However, P intake would be maximized by eating solely herbs, and Na intake by feeding on roots only.

Foraging behaviour of free-ranging beavers

The free-ranging beavers spent a considerable amount of time per day foraging, feeding on average 2.7 h/day longer in the winter than in the spring or summer (table III). The time actually spent gnawing the food (Tg) was estimated from the relationship between the proportion of point observations spent feeding (pf) and the proportion of continuous observations spent gnawing the food (pg) in a subsample (n = 16, excluding 1 outlier). The relationship between these mutually variable data was better described by a geometric mean regression than by a linear regression (RICKER, 1984):

$$pg = 1.4698 \times pf - 0.3962 \qquad (r = 0.590,\ p < 0.05).$$

Interpreting pf as Tf/Ta and pg as Tg/Ta, we estimated Tg from Tf and Ta, where Ta is the length of the active period (*i.e.* spent outside the den). The beavers appeared to spend a larger proportion of their foraging time gnawing food in the winter than in the spring or summer (table III). In other words, they used relatively less time to select and gather the food (per unit of food ingested) in the winter.

In all seasons, the beavers ate primarily woody food. In the winter, contrary to the model predictions, the beavers ate nearly exclusively bark (fig. 3). This diet was however satisfactory in three of the four winters. Although the intake rate of winter bark was low, the beavers could just obtain enough energy for maintenance within their foraging time limit, ingesting about as much energy as they expended. The Na requirement was just met by eating only a few roots. The P requirement, on the other hand, was amply met. The second winter was exceptional: the beavers spent much time on exploration, and they apparently ingested less energy than they expended. Intake was just enough to fulfil the P requirement, whereas the Na requirement was not met.

In the spring, the beavers ate woody food (twigs with adhering leaves 79% and bark 21% of wet weight) supplemented with some herbs, which was not in accordance with the model predictions (fig. 4a).

However, in two of the three years, this diet was again satisfactory: the beavers obtained more energy than they expended by foraging up to their time limit. They actually ingested more than enough P, and they also obtained more Na than they required. In the spring of the first year of the study, the beavers swam large distances exploring their new surroundings (NOLET & ROSELL, 1994), and the energy intake of the beavers was apparently less than the energy expenditure. They ate just enough to satisfy their P and Na requirements.

In the summer, the beavers again chose mainly woody food (twigs 59%, bark 41%) supplemented with some herbs. This food choice was close to the diet predicted under foraging time minimization in all three years in which the diet was studied (fig. 4b). The beavers ingested about as much energy as they expended in all years. Both the P and Na requirements were amply met.

DISCUSSION

Failure to predict diet choice in the winter and spring

Non-woody foods were predicted by the linear programming model to be eaten by beavers in the winter and spring, but were actually largely ignored. This discrepancy might be due to some bias in the parameter estimates. For instance, the application of data derived from carrots to roots of non-domesticated plant species might result in an overestimation of the nutritional value of the latter. Apart from such errors, there are three possible reasons why the model failed to predict the diet correctly: (1) the constraints were inappropriate, (2) the foraging goals were inadequately defined, or (3) the beavers were not foraging in an optimal way.

Inappropriate constraints? We used a foraging time limit and an assimilation limit instead of the digestive constraint successfully used by BELOVSKY (1984b) and DOUCET & FRYXELL (1993) to model the diet choice of American beavers. These authors considered the filling effect of forages to equal their bulkiness (wet mass/dry mass) multiplied by their retention time. HOBBS (1990) criticized the use of bulkiness in the formulation of the digestive constraint, because of the differential passage rates of fluids and solid particles. In hindgut fermenters, such as the beaver, fluid is flushed through the stomach more rapidly than solid particles, but is is retained longer in the caecum (BJÖRNHAG, 1972; PICKARD & STEVENS, 1972; CHILCOTT & HUME, 1985). It is therefore unlikely that—food retention time being equal—the fresh food intake is independent of the proportion of dry matter of the food. In fact, we found a negative correlation between these two variables in beavers.

Hence, the filling effect of a forage does not seem to be simply proportional to its bulkiness.

The strong negative relationship between the daily dry matter intake and the mean retention time in American beavers reported by DOUCET & FRYXELL (1993), indicates that the digestive capacity is largely determined by the passage rate of the solid food particles. However, in their study the mean retention time of the preferred tree species (*Populus tremuloides*), a herbaceous plant (*Rubus idaeus*), and an aquatic (*Nymphaea odorata*) did not differ significantly, indicating that the digestive capacity was not different per food type. Considering these arguments, we did not use the digestive constraint.

However, since the allometric-based assimilation limit used in our study was derived from animals at peak lactation, it may not be appropriate for maintenance conditions. SIBLY *et al.* (1990), for instance, showed that the gut capacity in rabbits (*Oryctolagus cuniculus*) was larger during lactation than at other times of the year. Recently, FRYXELL *et al.* (1994) showed that the difference in *ad libitum* intake of two tree species by American beavers could be explained by the difference in their food retention times. Therefore, the retention times of the food types used in our study should be measured in order to test if they do not differ, and whether a digestive constraint based on food passage rate (ignoring differences in bulkiness) is limiting food intake in beavers after all.

Plant defences were not specifically incorporated in the present model, but it was evident from our feeding trials that the non-woody food plants were simply unpalatable. It has long been recognized that anti-herbivore plant defence affects food choice in herbivores (FREELAND & JANZEN, 1974). From the observation that beavers prefer the less resinous aspen and willows to alder and conifers, BRYANT & KUROPAT (1980) already inferred that the beaver's food choice among woody species may be controlled by plant secondary compounds. Phenolics and a yet unidentified secondary compound in aspen trees were shown to deter beavers (BASEY *et al.*, 1988, 1990). In order to explain the discrepance between predicted and actual use of water lily by beavers, DOUCET & FRYXELL (1993) also speculated about the role of plant defences, suggesting that low concentrations of such compounds might make water lily more palatable that the other food plants tested.

In our case, the roots of *Iris pseudacorus* contain great concentrations of tannins (HEGNAUER & HEGNAUER, 1962-1992), which have been shown to have a repellent effect in ruminants (ROBBINS *et al.*, 1987) (but, interestingly, not in specialized hindgut fermenters; MCARTHUR & SANSON, 1991). Herbs might be largely avoided because of their great K concentration relative to the Na concentration, which would disturb

the K:Na balance in the animal (ROBBINS, 1983; MICKELSON & CHRISTIAN, 1991). Herbaceous species also tend to contain alkaloids (HEGNAUER & HEGNAUER, 1962-1992). The alkaloid desoxynupharidin of *Nuphar lutea* was demonstrated in the secretion from the castor-gland in beavers along the Elbe, suggesting that beavers can adapt to the intake of some of these compounds (LUCKNER, 1969). Future models of diet choice of beavers, or indeed any generalist herbivore, should account for the palatability of food plants. SCHMITZ *et al.* (1992) present a first attempt.

Inadequate foraging goals? We used the maximization of the intake rates of metabolisable energy (MEI), nitrogen, phosphorus or sodium and the minimization of the foraging time as the foraging goals. By using MEI instead of the net energy intake (= MEI minus the heat increment of feeding, generally considered the primary goal in optimally foraging animals; STEPHENS & KREBS, 1986), we implicitly assumed that the heat increment of feeding did not vary among food types. We do not think that the model predictions would have been very different under NEI (instead of MEI) maximization. However, recent studies have indicated that in some cases animals in fact strive to maximize efficiency rather than rate (TOLKAMP & KETELAARS, 1992; YDENBERG *et al.*, 1994). In order to evaluate this foraging goal (efficiency maximization), measurements of the energetic costs of gathering and processing, and the heat increment of feeding per food type are essential.

Non-optimal foraging? In the summer, the beavers seemed to minimize feeding time by mainly eating woody food. However, in the winter and spring, the beavers were possibly not foraging in an optimal way, because they were not (yet) fully adapted to their new surroundings.

Unfortunately, diet choice has not been quantified along the Elbe (where the beavers originated from). However, HEIDECKE (1988) enumerates the food plants which are used more or less frequently: the beavers primarily feed on *Populus* and *Salix* trees and shrubs, but in the summer season, they often eat herbaceous species of pioneer communities (*Chenopodium, Polygonum, Rumex*, and *Rorippa* spp.) and aquatics (*Nymphaea alba* and *Nuphar lutea*). In the Biesbosch, these non-woody food plants of beavers virtually disappeared together with other aquatic and pioneer plant species due to the closure of the main entrance to the sea in 1970 (ZONNEVELD, 1960; DE BOOIS, 1982).

After release in the Biesbosch, the beavers might have compensated for the lack of their favourite herbs and aquatics by spending more time feeding on woody plants. Woody plants were so easily available that they were an attractive substitute at low cost. Although perhaps not optimal, the beavers' actual diet choice was satisfactory for maintenance conditions. The beavers had gained weight after a stay of at least

one year (NOLET, 1994). In addition, they did not show a preference for Na-impregnated sticks in the spring and summer, indicating that the beavers did not experience a Na deficit at that time of the year (NOLET, 1994).

Necessity of mixed diet for survival and reproduction

We hypothesized that beavers eat herbs and aquatics in order to meet their protein and Na requirements, respectively. We showed that, under maintenance conditions, the P and Na requirements did generally not act as constraints. Nevertheless, in the summer and autumn, they ate dead twigs which appeared relatively rich in Na. Moreover, the beavers showed a preference for non-willow woody species in the Biesbosch, which appeared to be relatively rich in P or Na (NOLET *et al.*, 1994). We also cannot exclude the possibility that the beavers were better in absorbing P from the food than the non-coprophagous herbivores from which the allometric relationship of P requirement was derived (PEHRSON, 1983). Actual intake of P and Na might therefore have been slightly greater than calculated intake. Thus, roots and herbs were not essential for Na or P (let alone protein) during maintenance, except in winter when only few roots were eaten as a supplement to bark in order to satisfy the Na requirement.

However, the reproductive rate of the beavers was low in the first five years after the translocation to the Biesbosch (NOLET, 1994). From our allometric relationships it was derived that during lactation the P and Na requirements are more than six times greater than during maintenance. Beavers thus seem to need herbs and aquatics as a complementary P and Na source, respectively, in order to reproduce. Further study is needed to reveal whether the lack of herbs from pioneer communities and dicotyledonous aquatics in the Biesbosch is the major cause of the low reproductive rate in this translocated beaver population (NOLET, 1994).

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